THE GENOTYPES OF MAIZE[1]

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The doctrine of evolution had to overthrow the conception of permanency of specific types, generally held when Darwin's "Origin of Species" was published, because that conception was then associated with the idea of a separate original supernatural creation of each such type. It was Darwin's great triumph that he succeeded in marshaling such an array of facts pertaining to variability, as to convince the scientific world—and through the scientific world, ultimately the whole world—that everything is in a state of flux, and that there is no such thing as permanency among living things.

Owing to the work of De Vries and the other early students of modern genetics, permanency of type again demands serious scientific consideration, for such permanency is no longer incompatible with the doctrine of evolution, being now associated with some form of the mutation theory. The old idea of the immutability of specific types was based upon almost total ignorance of genetics, as was likewise the Darwinian conception of fluidity and gradual change, for although many appeals were made by Darwin to the experiences of plant and animal breeders, it is now known that these experiences were the result of no such careful control of conditions or analysis of results as has been found necessary for the discovery of genetic laws. The critical work of the past few years has wrought a great change and the new idea of permanency is gaining ground with the growth of experimental knowledge.

Without granting that we have yet reached a position in which we can say definitely that types are absolutely

[1] Read before the American Society of Naturalists, December, 1910.

permanent and do not, at least in some cases, gradually change into something new, the large accumulation of

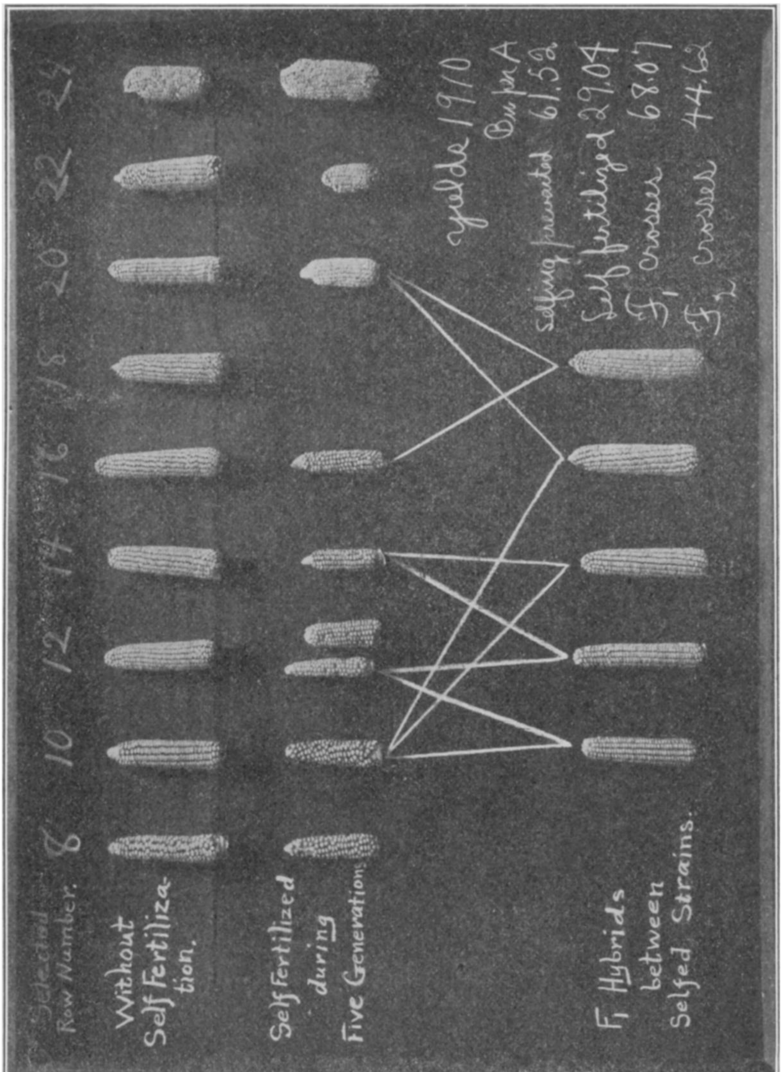

FIG. 1. Each ear in this exhibit represents a different pedigreed family. In each family the variation was slight, and the ear chosen for the exhibit was fairly representative of the entire family. The two self-fertilized ears under selection number "12" belong to two distinct strains, the left-hand one being my "Strain A" of other publications. During the last two years this has been selected to its own modal number, while the right-hand ear has been selected to twelve rows throughout the course of the experiments.

experimental data now available makes it necessary to recognize a clear distinction between the evolutionary changes in types, on the one hand, and the fluctuations within each type, on the other hand.

Quite naturally the first experimental evidence of the existence of permanent hereditary types involved only such characteristics as are clearly distinguishable upon inspection. Thus Jordan was able to demonstrate that within the systematic species *Draba verna* there are included as many as two-hundred hereditary forms, whose distinguishing characteristics appear unchanged from generation to generation, in such manner that his pedigrees of these forms were clearly and permanently distinguishable from each other by easily defined morphological features. Such "*petites espèces*" or "little species" (afterwards called by De Vries "elementary species," and by Johannsen "biotypes" or "genotypes"), have since been observed by Wittrock and his students, and by many others, in a great number of wild species, and they are now quite generally supposed to be of almost universal occurrence.

About 1890 N. H. Nilsson made a similar discovery in connection with his breeding of wheat, oats, barley and other grains at Svalöf, Sweden, but his work remained practically unknown to the scientific world until it was brought to light several years ago by De Vries. Nilsson found in these grains elementary species, each with its own morphological characters and its own specific capacity to yield crops of given size or quality under given external conditions. More recently, sharp-eyed taxonomists have been rapidly raising many of the elementary species of wild plants to the rank of systematic species.

It was natural that the earliest genotypes recognized, such as those of Jordan and Nilsson, should have possessed visibly discrete characteristics, and that they should first have become familiar in normally self-fertilized plants, among which little confusion is occasioned

by the rare crossing of unlike individuals. Great credit is due to Johannsen[2] for demonstrating that in such self-fertilized plants, types also exist which are not readily distinguishable by simple inspection, but whose occurrence may be completely demonstrated by the refined methods of the mathematician. Not only has Johannsen's work been so extensive as to justify the conclusions arrived at by him, but various other investigators, working with different classes of research material, have shown that the conditions found by Johannsen in beans and barley are duplicated in many other species and varieties. Perhaps the strongest support in this direction has come from the work of East[3] with potatoes and that of Jennings[4] with various microscopic organisms, especially with paramecium.

The fact that *Draba verna*, and many other wild species in which the existence of numerous elementary species has been demonstrated, as well as wheat, oats, barley and beans, are all predominantly self-fertilizing, and that potatoes and paramecium have an asexual reproduction, has led some to the erroneous notion that the discreteness, uniformity and permanence of the types which have been discovered among these and other similar organisms, are in some way dependent upon the absence of crossing.

It must be admitted that conclusions drawn from self-fertilized and asexual material do not necessarily apply to plants and animals whose successful existence is dependent upon repeated crossing. Nevertheless, the conception of pure and permanent genotypes in cross-bred material has become familiar simultaneously, owing to the work done in Mendelian heredity; for homozygous

[2] Johannsen, W., "Ueber Erblichkeit in Populationen und in reinen Linien," 68 pp., Jena, 1903.

[3] East, E. M., "The transmission of variations in the potato in asexual reproduction," Conn. Exp. Sta. Report 1909–1910, pp. 119–160, 5 pls.

[4] Jennings, H. S., "Heredity, variation and evolution in Protozoa—II. Heredity and variation of size and form in Paramecium, with studies of growth, environmental action and selection," *Proc. Amer. Phil. Soc.*, 47: 393–546, 1908.

combinations of the various characteristics of plants and animals "breed true" to those characteristics. Just as the first recognition of permanent differences in pure lines involved easily distinguishable characters, so also these first discoveries of permanent pure-breeding genotypes in cross-bred plants and animals involved easily definable morphological characteristics. The demonstration that in normally pure-bred lines there are distinctions more minute than such easily visible features as characterize the elementary forms of Draba and many other species, was an important advance in our analysis of the populations which make up the species of plants and animals. A similar demonstration that populations of cross-breeding plants and animals are composed of fundamentally distinct types, intermingled but not changed by panmixia, and capable of being separated by appropriate means and of being shown to possess the discreteness, uniformity and permanence already demonstrated for the genotypes of self-fertilized and clonal races, will add greatly to the importance of the fundamental conception of permanency of types involved in the work of De Vries and Johannsen.

For the study of this problem there is probably no better plant than Indian corn. It is known to exist in a large number of obviously distinct strains or subspecies which cross together with the greatest ease. Many of its characteristics have been proved by different investigators to be Mendelian unit-characters; such, for instance, as the color of the seed-coat, whether red, dark yellow, light yellow, variegated or colorless, the color of the aleurone layer, whether blue, red or white; the color of the endosperm, whether yellow or white; the chemical composition of the endosperm, whether starchy or sugary, the color of the silks and cobs whether red or white, etc. It has become known also, mainly through the excellent work done at the Illinois State Experiment Station, that oil-content and protein-content of the grains, the position of the ears, the number of ears on the stalk, and

several other characters, are capable of accentuation by selection, so that different degrees of these qualities are capable of being made characteristics of particular strains of corn, without there being the least evidence as yet that these last-mentioned qualities bear any relation to the unit-characters with which the student of genetics generally deals. A further point in favor of maize as a subject for the study of genotypes among cross-breeding organisms lies in the fact that its flowers are so arranged that, while self-fertilization is possible, it is naturally almost completely excluded, thus ensuring the same relations as are presented by bi-sexual or diœcious plants and animals, while retaining the means of conveniently testing the genotypic nature of each individual by controlled self-fertilizations.

I think I have demonstrated during the last five years that there are many genotypes of Indian corn which, although they can not always be distinguished by definable external characteristics, can be proved to be just as certainly and permanently discrete as the types whose distinguishing features can be recognized as Mendelian unit-characters. I shall endeavor to show, in what follows, a portion of the evidence which leads me to this conclusion.

In 1905 I undertook a rather extensive series of comparisons between cross-bred and self-fertilized strains of Indian corn for the purpose of discovering the effects of these methods of breeding upon variability, and these investigations have been continued each year since that time. Two phenomena immediately attracted my attention: First, the well-known fact that the children of self-fertilized parents are inferior to those of cross-fertilized parents in height, yield and other characters dependent in any way upon physiological vigor. In every instance this phenomenon was plainly evident in the very first generation after self-fertilization. This decrease in physiological vigor due to self-fertilization has become an

extremely important relation in the study of the genotypes, as will be shown later.

The second phenomenon which quickly made itself manifest, was first clearly appreciated in the second generation after the beginning of the experiments; this was the fact that each self-fertilized family possessed morphological features which clearly differentiated it from all other families. In most cases the distinguishing characteristics of these families were of such elusive nature that it was impossible to recognize definite unit-characters, and indeed, morphological descriptions of the several pedigrees could often be made only in terms of greater or less intensity of the several qualities exhibited. However, the distinctions were real and applied to every member of the particular family. Thus one family might have a very slender, poorly developed male panicle, while another would have more thick and dense branches of the panicle. This difference might be quite small when given in actual measurement but inspection showed that every individual of the one family had the slender, illy developed panicles, while all of the offspring of the other family had the thicker, denser type. Similarly, one family might have a slightly broader and darker green leaf than another, and these characteristic differences were likewise uniformly present in all members of the single families contrasted. No such character as this is capable of being traced through the generations following a cross, in the manner usually pursued by the geneticist, and the matter must be approached by indirect methods. The important point to be kept in mind here is simply that *the self-fertilized families, derived originally from a common stock, do differ by morphological characteristics,* and that there comes to be great uniformity in regard to the presence of these characteristics in all the individuals of a given self-fertilized family.

This relative uniformity, which is so obvious even to the casual observer, is not sufficient in itself, however,

to positively demonstrate the existence of distinct genotypes in maize, because the slight variations which must always be present even in the most uniform progeny, can not be certainly distinguished as genotypic or fluctuating simply by inspection. Such demonstration must rest upon a combination of biometric and genetic evidence in order to prove acceptable. Most of the differentiating characters of my several strains of maize are such that they do not lend themselves readily to biometric methods, but the number of rows on the ear is well adapted for such study and several important results have been derived from the consideration of this character. An important proof that the self-fertilized families derived from my common original stock of corn are genotypically distinct, and that they do not owe their different morphological and physiological qualities to fluctuations within a single genotype, was quickly found in the fact that two of these families selected respectively to 12 and 14 rows of grains on the ears, showed a regression of row-number toward different centers instead of toward a common center. The mean of the original population was slightly above 14 rows. The selection to 14 rows was very near this mean and the selection to 12 rows was very near this mean and the selection to 12 rows considerably below it. According to Galton's well-known law of "regression toward mediocrity," the mean of a family whose parents were selected to 12 rows should have lain somewhat above 12 rows, and that selected to 14 rows should have retained the mean approximately at 14 rows. The actual result in the case of selection to 12 rows was the production of a family having a mean row-number considerably below the number of rows selected, and the subsequent generations have since shown a close approach to an 8-rowed condition; while the family whose parents were in each generation selected to 14 rows has always had the mean very near to 14 rows. As these families were grown under as nearly uniform conditions as possible, the fact that the 14-rowed family continues

to have its mean row-number at 14 shows that the fall in row-number from 12 to 8 in the other family has been due to internal rather than to external causes.

The change in variability in number of rows on the ears has also been studied from year to year. Continued self-fertilization has resulted in a gradual decrease of variability in the number of rows per ear in each of the self-fertilized lines. This is a fluctuating character, and so far as present evidence goes, the number of rows per ear in any strain can not be fixed at a definite number. While it is probable that none of my self-fertilized families has yet reached an absolutely pure-bred condition, several of them have become so nearly pure-bred that their various relations can be used to demonstrate that they are approaching purity as a limit.

In 1909 two of these nearly pure-bred families were compared with their reciprocal hybrids in the first and second generations, with reference to the variability in number of rows.[5] It was found that the average variability in these two self-fertilized families was 9.08 per cent. The variation in number of rows in their F_1 progeny was 9.06 per cent., and in the F_2 12.63 per cent. A comparison of these coefficients of variability shows at once that the variation in number of rows in the F_1 is essentially identical with that in the self-fertilized lines used for the cross. Theoretically this should be so if the strains used were pure genotypes, because in that case all germ-cells in each pure strain were alike, and therefore, when individuals belonging to these two lines were crossed, equal sperms met equal eggs; consequently there should be no variability in their offspring due to germinal differences, but only those due to environment in the widest sense. As the pure-bred families and their F_1 and F_2 progenies were grown beside each other during the same season, they were subjected to as nearly identical environmental influences as can be attained.

[5] Shull, G. H., "Hybridization methods in corn breeding," *Am. Breeders' Magazine*, 1: 98–107, 1910.

Consequently, when the F_1 shows the same variability as the pure lines which entered into it we must conclude that there was at least approximate equality among the sperms which came from the one self-fertilized strain, and among the eggs which came from the other. In the F_2, on the other hand, genotypic differences appear, owing to the segregation of the different characteristics into the different germ-cells, and to this fact may be ascribed the increased variability in the F_2.

While other characters have not been studied by the same methods that have been used in the investigation of the number of rows on the ears, several features associated with the physiological vigor of the various pedigrees have given evidence which appears to me to be strongly corroboratory of the uniformity of the germ-cells produced by plants which have become pure-bred through continued self-fertilization. The smaller size and less vigor of the offspring of self-fertilized plants as compared with those from a normally cross-bred plant were formerly taken to indicate that self-fertilization is injurious, and Darwin's "Effects of Cross and Self-fertilization in the Vegetable Kingdom" strongly impressed this point of view. I have been able to demonstrate, however, that this supposedly injurious effect of self-fertilization is only apparent and not real; or at least that if there is such injurious effect, it is relatively insignificant as compared with the increased vigor due to heterozygosis. The most important evidence of this is found in the fact that the continuation of self-fertilization in any pedigree does not produce a corresponding decrease in vitality and size. The decrease resulting from a second year of self-fertilization is not as great as that from the first year. The third year of self-fertilization produces still less deterioration, and as this process is continued a limit is approached in such manner as to justify the inference that when complete purity is attained no further deterioration is to be expected, thus proving that self-fertilization is not in itself injurious.

That this is also true of other plants is derivable from Darwin's own work.

This decrease in size and vigor is accompanied by the gradual lessening of variability, and when that state is finally reached in which there is no further decrease in size and vigor, it seems probable that there will be also no further noticeable change in variability. This does not mean, of course, that there will be no variability, for even the most uniform group of plants or animals will of necessity show slight variations produced by different conditions of life, food supply and so forth. But present evidence does not warrant the belief that such fluctuations affect in the least the fundamental qualities of the genotype.

In 1908 I suggested a hypothesis to explain the apparent deterioration attendant upon self-fertilization, by pointing out that in plants, such as maize, which show superiority as a result of cross-fertilization, this superiority is of the same nature as that so generally met with in F_1 hybrids. I assumed that the vigor in such cases is due to the presence of heterozygous elements in the hybrids, and that the degree of vigor is correlated with the number of characters in respect to which the hybrids are heterozygous. I do not believe that this correlation is perfect, of course, but approximate, as it is readily conceivable that even though the general principle should be correct, heterozygosis in some elements may be without effect upon vigor, or even depressing. The presence of unpaired genes, or the presence of unlike or unequal paired genes, was assumed to produce the greater functional activity upon which larger size and greater efficiency depend. This idea has been elaborated by Dr. East[6] and shown to agree with his own extensive experiments in self-fertilizing and crossing maize. He suggests that this stimulation due to hybridity may be analogous to that of ionization.

Mr. A. B. Bruce proposes a slightly different hypothe-

[6] East, E. M., "The distinction between development and heredity in in-breeding," AMER. NAT., 43: 173–181, 1909.

sis in which the degree of vigor is assumed to depend upon the number of *dominant* elements present rather than the number of *heterozygous* elements. While all of my data thus far are in perfect accord with my own hypothesis, and I know of no instance in which self-fertilization of a corn-plant of maximum vigor has not resulted in a less vigorous progeny, it is quite possible that I have still insufficient data from which to distinguish between the results expected under these two hypotheses. However, for the purpose of the present discussion, it is not necessary to decide which of these two hypotheses (if either) is correct. Both of them are based upon the view that the germ-cells produced by any plant whose vigor has been increased by crossing are not uniform, some possessing positive elements or genes not possessed by others.

Several different characters which are more or less dependent upon physiological vigor have been taken into account in my work, each of which gives its own support to the conception upon which both of these hypotheses are based. The number of rows of grains on the ears which has been most extensively used as a measure of variability, and as a guide in selection, is found to be somewhat affected by the vigor of the individual, and it is due to this fact, no doubt, that the row-number is a fluctuating character, even in the pure genotype. Another characteristic which has been used as a measure of vigor has been the yield of corn computed in bushels per acre.[7] A third characteristic, which was not taken into account at the beginning of the experiments but which has given confirmatory data in the later years, is the height of the stalks, a character which was much used by Darwin as a measure of vigor in his study of the effects of cross- and self-fertilization in plants.

[7] It should be understood that this method of stating yields is seriously defective, in that it implies the existence of a much smaller probable error than is actually present, since each of my pedigrees has usually occupied only about one one-hundredth of an acre. However, I believe that this defect is more than offset by the advantage of using a unit of yield with which all readers are familiar.

We may now consider the behavior of these several measures of physiological vigor in relation to the theory that distinct genotypes of maize are gradually segregated from their hybrid combinations, by self-fertilization, and that the degree of vigor is correlated with the degree of heterozygosis.

I have kept families selected to given numbers of rows on the ears—one series of families repeatedly self-fertilized and another series repeatedly crossed with mixed pollen in such a manner that self-fertilization is precluded by artificial means. It is not practicable to do this crossing with mixed pollen in such a manner as to duplicate the conditions found in an ordinary corn-field for the simple reason that the number of individuals which contribute the pollen must be more greatly restricted than is true in the open field. While self-fertilization has been entirely prevented, there has been a degree of in-breeding somewhat greater therefore than will occur under non-experimental conditions. This degree of in-breeding is sufficient to slowly eliminate some of the hybrid elements which were originally in my strain of corn and should consequently lead to a gradual deterioration in case my theory of the relation between vigor and hybridity is correct. As a matter of fact, such deterioration has become apparent in the "cross-bred"[8] families, when measured either by height of stalk or yield per acre, though both of these measures show that the deterioration has been slight. It is so slight, indeed, that it is very much exceeded by the fluctuations from season to season, and may only be demonstrated by the application of a correction which approximately eliminates this seasonal fluctuation. When we compare this continual slight fall in physiological vigor of the cross-

[8] It should be noted that here and in what follows I use the expression "cross-bred" in a special sense, to denote the fact that all self-fertilization has been avoided. The more usual use of the term "cross-bred" to denote a cross between individuals belonging to distinct strains, I replace in this paper by the expression "F_1," as I can see no tangible distinction between such a cross, and hybridization in the older, more restricted, and more arbitrary sense.

bred families with the changes produced in the self-fertilized families during the same period, there is a striking contrast, for in the latter case there was great decrease in height and yield in the first year, a considerably less decrease in the second year of self-fertilization, still less in the third year, and so on, and while I have evidence that none of my self-fertilized families has yet reached a state of perfect stability, they are at the present time decreasing in regard to both of these measures of vigor somewhat less rapidly under continued self-fertilization than are the families in which self-fertilization has been absolutely precluded.

Necessary corollaries of the view that the degree of vigor is dependent on the degree of hybridity, or, in other words, that it is dependent roughly upon the number of heterozygous elements present and not upon any injurious effect of in-breeding *per se,* are (*a*) that when two plants in the same self-fertilized family, or within the same genotype, however distantly the chosen individuals may be related, are bred together, there shall be no increase of vigor over that shown by self-fertilized plants in the same genotype, since no new hereditary element is introduced by such a cross; (*b*) that first generation hybrids produced by crossing individuals belonging to two self-fertilized lines, or pure genotypes, will show the highest degree of vigor possible in progenies representing combinations of those two genotypes, because in the first generation every individual will be heterozygous with respect to all of the characters which differentiate the two genotypes to which the chosen parents belong, while in subsequent generations, recombination of these characters will decrease the average number of heterozygous genes present in each individual; (*c*) that crosses between sibs among the first-generation hybrids between two genotypes will yield progenies having the same characteristics, the same vigor, and the same degree of heterogeneity, as will be shown by the progenies of self-fertilized plants belonging to the same first-generation family.

All of these propositions have now been tested in a limited way. In 1910 nine different self-fertilized families were compared with nine crosses between sibs within the same self-fertilized family; ten crosses between sibs in F_1 families were compared with ten self-fertilizations in the same F_1 families; seven families were raised as first generation hybrids between individuals belonging to different self-fertilized families; and ten families were grown, in which self-fertilization had been entirely precluded during the past five years. The average height of plants in decimeters, the average number of rows per ear, and the average yield in bushels per acre, in these fifty-five families are given in the following table:

	Selfed $\times$ Self	Selfed $\times$ Sibs	F_1	F_2	$F_1 \times$ Self	$F_1 \times$ Sibs	Cross-breds
Av. Height	19.28	20.00	25.00	23.42	23.55	23.30	22.95
Av. Rows	12.28	13.26	14.41	13.67	13.615	13.73	15.13
Av. Yield	29.04	30.17	68.07	44.62	41.77	47.465	61.52

An examination of this table indicates to me that on the whole my self-fertilized families are not yet quite pure-bred; for the sib crosses give on the average a slightly greater height, number of rows per ear, and yield per acre than the corresponding self-fertilized families, as shown by a comparison of the first two columns of the table. The same fact is apparent from a comparison of the "$F_1 \times$ self" and "$F_1 \times$ Sibs" columns, except that in this case the heights and number of rows per ear are essentially equal while the yield per acre is significantly higher in the sib-crosses than in the self-fertilized families. An alternative explanation of these slight differences between the results of self-fertilization and of sib-crosses may attribute them to an injurious effect of self-fertilization, but in any event such injurious effect must be exceedingly slight as compared with the stimulating effect of heterozygosis. My practise of choosing for seed the best available ears tends to delay the attainment of complete genotypic purity, and this fact favors the view that whatever advantages the sib-

crosses show, are attributable to this lack of purity, rather than to any advantage gained by crossing *per se*.

The columns of the table representing the F_1 and F_2 show very plainly the superiority of the former over the latter in regard to both height and yield per acre. The fall in average height from F_1 to F_2 from 25 decimeters to 23.4 decimeters and the corresponding fall in yield per acre from 68.07 bushels in the F_1 to 44.62 bushels per acre in the F_2 show in a most striking way the economic advantage of using first-generation hybrids for producing the corn crop. A comparison of the F_1 hybrids with the "cross-breds" shows the average yield of the former to be 6.55 bushels per acre greater than that in the families in which self-fertilization had been avoided.

The relation of these results to the experiences of economic breeders of corn may now be considered. Perhaps in no other class of plants has the evidence been so strong for the possibility of gradual improvement through continued selection as in corn, and this method has been generally followed. The selections of particular physical and chemical qualities which have been carried on at various experiment stations have produced noteworthy results. Most important instances of this kind are involved in the breeding experiences of Hopkins, Smith and other breeders at the Illinois State Experiment Station, which have been already mentioned. Here selections for high oil content, low oil content, high protein and low protein, high ears and low ears, and the angle which the ears make with the axis of the plant, as well as selection for increased yields, have all led to the production of strains which possessed the desired qualities to a much higher degree than that in which they existed in the foundation stock when the selection began. All of these results may be readily explained on the ground that some hybrid combinations of genotypes have greater capacity for the production of the desired qualities than other combinations, and that the selection has gradually brought about the segregation of those genotype-combinations

which had the highest capacity for the production of the desired qualities. At least in regard to yield and not improbably also in regard to the other qualities for which selections were made, the results were dependent, not upon the isolation of pure types possessing the desired quality, but upon the securing and maintaining the proper combination of types. I have shown above that segregation takes place in a manner at least similar to, if not identical with, the well-known behavior of Mendelian characters. As a consequence of this, no strain of corn can be maintained at a high value with respect to any quality whose development is correlated with heterozygosis, except by continued selection for the particular qualities desired. If in any such specialized strain selections should be made for a few years on the basis of some character independent of the one used in establishing the strain, the superior qualities for which it was originally selected would quickly disappear, owing to the breaking up of the efficient combinations which had been segregated and maintained by selection.

The principles here presented have very great potential consequence for the practical grower of corn, and possibly for the breeder of many other cross-breeding plants and of animals. Their importance seems not to have been fully appreciated by any one however, until recently, though several breeders appear to have glimpsed the possibilities at one time or another. Thus G. N. Collins,[9] of the United States Department of Agriculture, has recently shown that several breeders at different times began experiments to test the value of hybridization in the production of high-yielding strains of corn. The first attempt of this kind which he has found was that of W. J. Beal[10] at the Michigan Agricultural College in 1876. At Professor Beal's instance several other experiment stations undertook to work in co-operation with the Michigan Station in testing the value of hybrids in

[9] Collins, G. N., "The value of first generation hybrids in corn," Bull. 191, U. S. Bureau of Plant Industry, 45 pp., 1910.

[10] Beal, W. J., Reports, Michigan Board of Agriculture, 1876–1881.

corn breeding, but only Professor Ingersoll,[11] of Purdue University, reported results. Professor Sanborn[12] apparently performed similar experiments in the late eighties at the Maine Agricultural Experiment Station. In 1892 G. W. McCluer[13] reported on a number of crosses made during the preceding two years at the Illinois Agricultural Experiment Station, and during the next two years Morrow and Gardner[14] published bulletins from the same station, describing the results of a number of crosses. Apparently none of this work led to the subsequent utilization of hybridization methods in corn breeding, as no work along this line appears to have been done between the time when Morrow and Gardner issued their second bulletin in 1893 and the publication of the first report of my work with corn at the Station for Experimental Evolution in 1908. The work of Beal, Ingersoll, Sanborn, McCluer, and Morrow and Gardner showed that increased yields from the hybrids, as compared with the strains used for the crosses, are the almost invariable result, though both McCluer, and Morrow and Gardner found isolated instances in which the hybrids were inferior to the parent strains. Hartley[15] has since reported that among a number of crosses made by the United States Department of Agriculture also, some gave poorer yields than the parent strains used for the cross, while others gave superior yields, and reached the conclusion, which I think is justified by my own results, that promiscuous crossing is not necessarily advantageous but that certain combinations lead to increased yields while others may prove disadvantageous. Collins[16] has

[11] Seventh Annual Report of Purdue University, 1881, p. 87.

[12] Sanborn, J. W., ''Indian corn,'' Agriculture of Maine, 33d Annual Report, Maine Board of Agriculture, 1889–90, p. 78.

[13] McCluer, G. W., ''Corn crossing,'' Bull. 21, Illinois Agr. Exp. Sta., 1892, p. 85.

[14] Morrow, G. E., and Gardner, F. D., Bulletin 25, pp. 179–180, and Bulletin 31, pp. 359–360, Illinois Agr. Exp. Sta., 1893 and 1894.

[15] Hartley, C. P., ''Progress in methods of producing higher yielding strains of corn,'' Yearbook, U. S. Dept. Agr., 1909, pp. 309–320, 4 pls.

[16] *Op. cit.*

also reported on sixteen hybrid combinations all but two of which gave increased yields in the F_1. From the work of all these men, especially from my own comparisons between F_1 and F_2 hybrids, it has become obvious that the secret of the highest success in corn breeding from an economic point of view lies in finding those strains which will produce the largest yield and then utilizing the first-generation hybrids each year.

The point which most interests us on the present occasion is not, however, the economic importance of using first generation crosses, but the evidence which appears to me clearly indicate that a normally cross-bred plant like Indian corn harmonizes in its fundamental nature with such normally self-fertilized material as beans, wheat and other grains, and such clonal varieties as potatoes, paramecium, etc., that the egg-cells and sperm-cells of even the most complex hybrids present a limited number of different types which can be assorted into homozygous combinations, and that, therefore, the progressive change resulting from continued selection may be simply explained as the gradual segregation of homozygous types or of the most efficient heterozygous combinations.

The fact that yield and perhaps many other qualities attain their highest development in the case of complex hybrids naturally leads to the unconscious selection of heterozygous plants for the next year's cultures, and the continual breaking up of these complex hybrids in subsequent generations gives a result which closely resembles fluctuating variation, but which is fundamentally different from it. The genuineness of the gains made by selection in corn might naturally lead to the conclusion that fluctuations are inherited were it not for the abundant evidence now available showing that a considerable portion of the variation presented is not fluctuational, but is due to the presence of a mixture of different types which any selection partially segregates.